

Research Article

Baseline studies on meiofauna in the Baltic Sea before bottom-trawl fisheries exclusion II. A comparative study using multi-gene metabarcoding and morphology

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Abstract

Understanding how meiofaunal communities respond to spatial protection measures is essential for evaluating the effectiveness of marine conservation strategies, particularly in heavily impacted regions such as the Baltic Sea. Here, we present one of the first integrated assessments of meiofaunal diversity across marine protected areas (MPAs) and adjacent reference areas (REFs) in the Baltic Sea. Our study combines whole-community metabarcoding of two genetic markers—mitochondrial COI and ribosomal 18S—with classical morphological identification of harpacticoid copepods. Sampling was conducted in the Fehmarn Belt and Oderbank regions as part of the DAM pilot mission MGF Ostsee, prior to the exclusion of mobile bottom-contact fishing. We provide a valuable baseline of community composition under current conditions. Results highlight strong complementarity between the genetic markers: 18S offered broader taxonomic coverage and higher alpha diversity, particularly for Nematoda and Platyhelminthes, while COI enabled more precise species-level resolution, especially for Copepoda. Spatial analyses revealed distinct assemblages between Fehmarn Belt and Oderbank, with notably higher copepod diversity in Fehmarn Belt. Significant differences between MPAs and REFs were detected only in Oderbank. Morphological and molecular datasets showed substantial but incomplete overlap, with each method capturing unique taxa, demonstrating their combined value for comprehensive biodiversity assessments. Our findings suggest that meiofauna communities reflect both regional environmental gradients and high small-scale patchiness. This study underscores the utility of multi-marker metabarcoding alongside traditional taxonomy for monitoring meiobenthic diversity and highlights the importance of incorporating meiofauna into long-term ecological assessments. The dataset provides a crucial reference point for evaluating future recovery and management outcomes following trawling exclusion.

Key words: Baltic sea, harpacticoid copepods, marine protected areas, meiofauna, MGF-Ostsee, multi-gene metabarcoding



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Introduction

Meiofaunal communities—comprising organisms passing through a 1-mm sieve but being retained in a 40- μ m sieve—are fundamental components of benthic marine ecosystems. They play vital roles in nutrient cycling, organic matter decomposition, and secondary production (Danovaro et al. 2008). Meiofauna plays a key ecological role by transferring energy from microbial producers and detritus to higher trophic levels, serving as an important food source for juvenile stages of various benthic metazoans including fishes (Giere 2009; Schückel et al. 2013). Beyond their trophic significance, meiofaunal communities are increasingly recognized as sensitive indicators of ecosystem health and early responders to environmental shifts and their diversity and structure often exhibit rapid and pronounced changes in response to stressors (Vassallo et al. 2006; Mokievsky et al. 2010; Zeppilli et al. 2015; Kim et al. 2020). Despite their ecological importance, meiofauna have long been underrepresented in biodiversity assessments, primarily due to the technical complexity and taxonomic expertise required for traditional morphological identification (Maximov et al. 2017). Consequently, our understanding of their diversity, ecological functions, and responses to anthropogenic stressors remains limited, particularly in heavily impacted environments such as the Baltic Sea (Bradshaw et al. 2021).

The Baltic Sea—with its pronounced salinity gradients, history of eutrophication, and legacy of industrial impacts—offers a unique setting for studying faunal responses to environmental stressors. Among the various anthropogenic pressures, mobile bottom trawling fisheries (Mobile grundberührende Fischerei, MGF) is a dominant driver of benthic change, exerting greater influence on seafloor ecosystems than most other stressors (Lampadariou et al. 2005; Micallef et al. 2018; Grip and Blomqvist 2020; Schönke et al. 2022). Bottom trawling physically disrupts seabed habitats and alters community composition, with well-documented impacts on larger benthic fauna (Schratzberger et al. 2002; Schratzberger and Jennings 2002; Clark et al. 2019; Bradshaw et al. 2021, 2024). However, its influence on sediment resuspension and biogeochemical cycling is less frequently examined (Bradshaw et al. 2021), and the response of smaller size classes—such as meiofauna—remains ambiguous, often attributed to their high resilience and rapid turnover rates (Schratzberger et al. 2002; Ingels et al. 2014). Despite their sensitivity to environmental disturbances and potential as bioindicators, meiobenthic communities have been relatively overlooked in impact assessments. This is particularly surprising given their known responses to anthropogenic stressors and established utility in ecological monitoring (Gray 1971; Marcotte and Coull 1974; Moore and Bett 1989; Kennedy and Jacoby 1999; Schratzberger et al. 2000, 2002; Schratzberger and Jennings 2002). Recent evidence suggests that long-term bottom trawling can substantially alter meiofaunal composition and energy flow within benthic ecosystems (Ingels et al. 2014).

In light of accelerating biodiversity loss and climate change (Chapin et al. 2000; Singh et al. 2021; Hochkirch et al. 2023), the establishment of marine protected areas (MPAs) has become a widely adopted strategy for safeguarding marine biodiversity. In the Baltic Sea, MPAs have been designated to mitigate the effects of bottom trawling, with MGF officially excluded from these zones since 18 December 2024 (Amtsblatt der Europäischen Union, DE, Reihe

L: Delegierte Verordnung (EU) 2024/2943 der Kommission vom 17. September 2024, 28.11.2024). Nonetheless, the effectiveness of MPAs in protecting benthic biodiversity—particularly that of meiofauna—remains underexplored.

This study contributes to the German Marine Research Alliance (Deutsche Allianz Meeresforschung, DAM) pilot mission MGF-Ostsee, which aims to evaluate the ecological effects of excluding MGF from Natura 2000 sites within Germany's Exclusive Economic Zone (EEZ) of the Baltic Sea. Within this initiative, work package 2.4 specifically investigates the impacts of bottom trawling on meiobenthic communities. A core component of this investigation involves a comparative assessment between MPAs and adjacent reference areas (REFs) in the Fehmarn Belt (FB) and Oderbank (OB) regions. In the first phase of the study (MGF Ostsee-I), a comprehensive inventory of local meiofauna was established using both classical morphological techniques and high-throughput whole-community metabarcoding.

Recent advances in DNA metabarcoding have revolutionized biodiversity assessments by enabling high-throughput, fine-resolution characterization of entire communities. However, limitations such as primer bias, incomplete reference databases, and marker-specific taxonomic gaps necessitate the use of multiple genetic markers. The mitochondrial COI and ribosomal 18S genes are widely applied in meiofaunal research, each offering distinct advantages. COI provides superior taxonomic resolution, often to species level, but can suffer from primer mismatches and uneven amplification across taxa. In contrast, 18S rDNA—particularly hypervariable regions such as V1–V2, V4 or V9—offers broader taxonomic coverage and more consistent amplification, albeit typically at lower taxonomic resolution (Günther et al. 2018; Rossel et al. 2019; Kapshyna et al. 2024). To overcome the limitations of single-marker approaches, many studies advocate for combining multiple markers to improve detection rates and taxonomic confidence (e.g. Zhang et al. 2018). Based on these evidences, we employed a multigene approach using both COI and 18S (V1–V2) markers to obtain a more comprehensive and robust characterization of meiofaunal diversity in the Baltic Sea.

In this study, we present a detailed assessment of meiofaunal communities in the FB and OB regions of the Baltic Sea, comparing MPAs and REFs prior to the enforcement of bottom trawling restrictions. Focusing on harpacticoid copepods—one of the most dominant and ecologically important meiofaunal groups—we combined metabarcoding (COI and 18S) and morphological identification methods to:

1. Characterize the taxonomic composition and diversity of meiofaunal assemblages across MPAs and REFs;
2. Quantify congruence and discrepancies between morphological and molecular detection methods, particularly for harpacticoid copepods;
3. Evaluate the potential of MPAs to conserve meiofaunal diversity and maintain community structure.

By integrating spatial comparisons and complementary methodological approaches, this study offers critical insights into the value of meiofauna as bioindicators and advances the development of robust monitoring tools for marine conservation in a heavily impacted sea.

Methods

Sample collection and laboratory procedures

As part of the MGF Ostsee-I project and in preparation for whole-community metabarcoding, a total of 24 sediment samples were collected between 26 May and 3 June 2020, during the RV Elisabeth Mann Borgese cruise EMB 238/1 in the Fehmarn Belt (FB) region (Fig. 1). These included 12 replicates from MPAs and 12 from REFs. In the Oderbank (OB) region, an additional 26 stations were sampled during the EMB 267/1 cruise (1–16 June 2021), comprising 17 replicates from MPAs and 9 from REFs (Fig. 1). Meiofauna samples were collected using a multicorer equipped with 12 core liners (inner diameter 9.6 cm; area coverage per core, 74.2 cm²). The top five centimetres of sediment from two cores, along with the supernatant water (sieved through a 40-µm mesh), were transferred into Kautex vials and preserved in DESS (described by Yoder et al. 2006) at room temperature; upon arrival at the laboratory, all samples were stored at +4 °C. Sediment samples for metabarcoding were processed following the method of McIntyre and Warwick (1984), involving sieving through a 40-µm mesh and centrifugation with Kaolin and Levasil® (three times at 4,000 rpm for 5 minutes each). Samples were preserved in DESS at room temperature. From each sample of organisms, a 50 mL subsample was filtered using sterile glass fibre filters (2.7 µm pore size). Filters were rinsed with 96% denatured ethanol to remove DESS residues and transferred into sterile, DNA-free 1.5 mL Eppendorf tubes. The filters were then dried in a SpeedVac concentrator (Eppendorf) at 45 °C for one hour.

Genomic DNA was extracted using the E.Z.N.A.® Mollusc DNA Kit (Omega Bio-Tek) for Fehmarn Belt samples and the DNeasy PowerSoil Pro Kit (Qiagen) for Oderbank samples, following manufacturer protocols. The two DNA extraction kits were used in different sampling years; the E.Z.N.A.® Mollusc DNA Kit occasionally required additional purification to remove PCR inhibitors, while the DNeasy PowerSoil Pro kit yielded cleaner extracts without further processing. Extracted DNA was further purified using AMPure XP magnetic beads (Beckman Coulter) when necessary. DNA concentration was quantified using a Qubit fluorometer and Qubit dsDNA High Sensitivity Assay Kit (Thermo Fisher) prior further processes. Two target gene regions were amplified via real-time PCR: the mitochondrial cytochrome c oxidase subunit I (COI) and the V1–V2 hypervariable region of the nuclear 18S rDNA gene. Amplification was performed using the primer pair F04/R22 for V1–V2 (Blaxter et al. 1998) and mLCOIintF/jgHCO2198 for COI (Geller et al. 2013; Leray et al. 2013), each tagged with partial Illumina Nextera adapter sequences. An indexing qPCR was conducted to attach Illumina Unique Dual Nextera Indexes and compatible Illumina adapters to each sample's amplicons. PCR reactions were performed in 20 µL volumes with 10 µL SsoAdvanced Universal SYBR Green Supermix (Bio-Rad), 1 µL of each primer (10 pM/µL), 2 µL of template DNA, and 6 µL of molecular-grade water. Thermal cycling conditions included an initial denaturation at 98 °C for 2 minutes, followed by 25 cycles of denaturation at 98 °C for 15 seconds, annealing at 54 °C (COI) or 57 °C (V1–V2), and elongation at 72 °C for 1 minute. The indexing PCR included 10 cycles with denaturation at 98 °C and combined annealing/extension at 72 °C for 45 seconds. Both PCRs included a melt curve analysis (65–99 °C) to

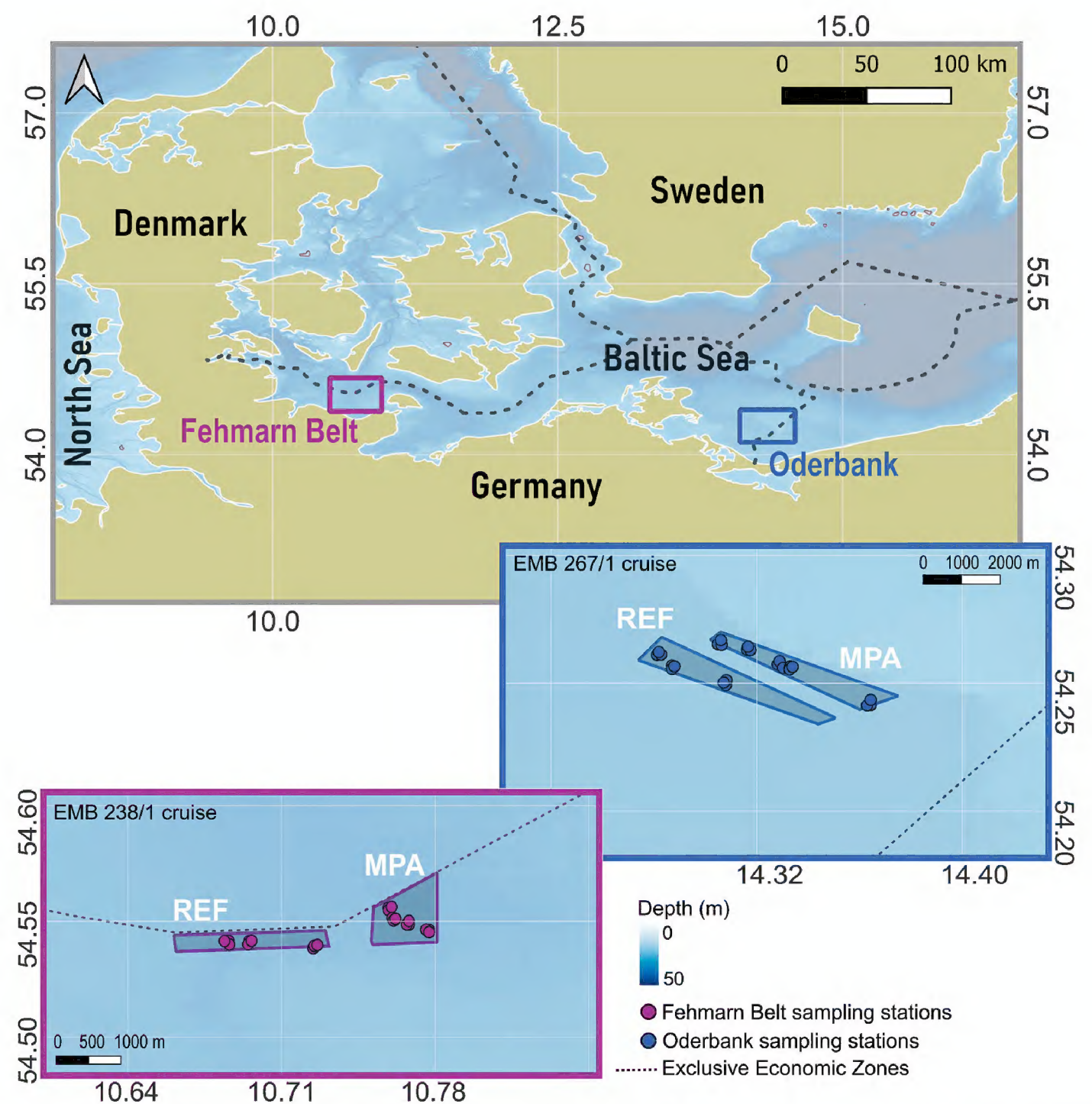


Figure 1. The upper map shows the two investigated areas, Fehmarn Belt (purple box) and Oderbank (blue box), and their geographical position within the Baltic Sea. The lower panels display the sampling stations collected with a multicorer during cruises EMB 238/1 (2020; Fehmarn Belt) and EMB 267/1 (2021; Oderbank), as well as the Marine Protected Area (MPA) and Reference Area (REF) in each region. Bathymetric data were obtained from GEBCO 2025, Natural Earth, and HELCOM. The map was generated in QGIS version 3.24.1-Tisler (code revision 5709b824).

assess amplification success in addition to Cq values and fluorescence signals. Indexed amplicons were pooled separately for each region and purified using 60% AMPure XP beads. Libraries were denatured and a 15% genomic PhiX spike-in was added prior to test sequencing using MiSeq Reagent Nano Kits v2 (250-cycle, paired-end). Final sequencing was performed using two Illumina MiSeq Reagent Kits v3 (300 cycles, paired-end) on an Illumina MiSeq platform at the DZMB Metabarcoding Laboratory in Wilhelmshaven, Germany.

To compare morphological and molecular assessments of harpacticoid copepod diversity, we conducted a parallel analysis using species-level identifications from morphology and compared these with metabarcoding results from both gene fragments. For the FB region, morphological data were taken from the published dataset of Packmor et al. (2025), which provides information on species richness based on microscopy. For the OB region, we used the final morphological identifications, including species richness data. The latest dataset is submitted in a forthcoming manuscript

(Ostmann, unpubl. data 1). Barcode reference sequences of morphologically identified harpacticoid copepods were generated from individual specimens in both regions and are submitted as part of a separate study (Ostmann, unpubl. data 2). These reference sequences enabled a comparison between morphologically confirmed taxa and metabarcoding detections across both areas.

Bioinformatics and diversity analyses

For community metabarcoding, demultiplexed sequencing reads from each gene fragment and sequencing run were trimmed to remove locus-specific primers using BMap (sourceforge.net/projects/bbmap/). Denoising and quality filtering were conducted with the DADA2 pipeline (Callahan et al. 2016). Sequences were truncated at 190 bp (R1) and 183 bp (R2) for COI, and at 212 bp (R1) and 200 bp (R2) for V1–V2, before merging the paired reads into contigs. Chimeric sequences were identified and removed. Amplicon Sequence Variants (ASVs) were de-replicated and taxonomically annotated using a custom pipeline—SGN Metabarcoding Pipeline (<https://github.com/pmartinezarbizu>) which incorporates the BLASTn tool. Each ASV was queried against the NCBI nucleotide database and the curated reference library of COI mtDNA and 18S rDNA barcodes from Ostmann unpub. data2. The top ten BLAST hits were retained, and metadata including percentage identity, query coverage, e-values, fragment length, GenBank accession number, and sample-specific read counts were recorded. Only true meiofaunal ASVs (belonging to Nematoda, Copepoda, Platyhelminthes, Arachnida, Ostracoda, Kinorhyncha, Gastrotricha, and Tardigrada) were retained for community analyses. For both sequencing runs ASVs from each gene fragment were merged and clustered into Operational Taxonomic Units (OTUs) using a neighbor-joining approach with a 3% similarity threshold for COI and V1–V2 using the R packages DECIPHER (Wright 2016) and dada2pp (Martínez Arbizu 2018). Taxonomic assignments were cross-validated against the World Register of Marine Species (WoRMS) database. The final curated OTU tables from COI and V1–V2 datasets were used for community analysis, employing a suite of R packages: ape (Paradis and Schliep 2019), ComplexUpset (Krassowski 2020), dada2pp (Martínez Arbizu 2018), dplyr (Wickham et al. 2023), effsize (Torchiano 2020), ggplot2 (Wickham 2016), ggpubr (Kassambara 2023), ggrepel (Slowikowski 2024), ggvenn (Yan 2023), pairwiseAdonis (Martínez Arbizu 2020), tidyverse (Wickham et al. 2019), UpSetR (Conway et al. 2017), and vegan (Oksanen et al. 2012).

Alpha diversity was assessed using OTU richness, Shannon diversity, and Pielou's evenness. Group differences were tested by Wilcoxon rank-sum tests and effect sizes were quantified using Cohen's *d*. These metrics were calculated separately for the V1–V2 and COI datasets to evaluate marker-dependent differences in diversity. Shannon diversity and evenness were computed based on number of reads per OTU as proxy for abundances. PERMANOVA was used to test for differences in meiofaunal community composition between regions (FB & OB) and areas (MPAs and REFs), while Sørensen and Jaccard similarity indices were calculated to quantify Harpacticoida community overlap between methods (COI, V1–V2 and morphology).

Results

Comparison of gene markers for meiofaunal community characterization

Two sequencing runs produced approximately 19 million paired-end reads from the V1–V2 and COI gene fragments, covering samples from both, FB and OB. Analysis of the COI dataset revealed 1,108 meiofaunal ASVs, which were clustered into 312 OTUs across both study areas. In comparison, the V1–V2 dataset yielded 2,946 meiofaunal ASVs, clustered into 1,425 OTUs. At the class level, both gene fragments detected a broad spectrum of meiofaunal taxa, including Chromadorea and Enoplea (Nematoda), Copepoda (primarily Harpacticoida and Cyclopoida), Arachnida (mites only), free-living Platyhelminthes, Ostracoda, Gastrotricha, Allomalorhagida (Kinorhyncha), and Tardigrada.

Fig. 2 illustrates the relative number of reads (Fig. 2A) and OTUs (Fig. 2B) for the major meiofauna groups based on metabarcoding data from both FB and OB. The V1–V2 marker identified Nematoda as the most diverse taxon, with 868 OTUs and the highest number of reads in both study regions. This was followed by Platyhelminthes (242 OTUs), Copepoda (110 OTUs), Ostracoda (100 OTUs), and Arachnida (29 OTUs), along with several less abundant taxa.

In contrast, the COI marker revealed generally lower overall diversity and number of reads across most groups. For Copepoda, OTU richness was nearly comparable between markers (105 OTUs in COI vs. 110 in V1–V2), while Arachnida (mites) were more strongly represented in the COI dataset (57 OTUs vs. 29 in V1–V2). Nematoda were dramatically underrepresented in the COI data, with only 79 OTUs detected, while Platyhelminthes and Ostracoda were represented by 34 and 16 OTUs, respectively. Alpha diversity metrics were calculated using read numbers as a proxy for relative abundances and revealed marked differences between the two markers (Fig. 3A–C). The V1–V2 dataset exhibited significantly higher OTU richness, Shannon diversity, and Pielou's evenness compared to the COI dataset (Wilcoxon $p < 2e-16$ for all comparisons, Fig. 3). On average, V1–V2 revealed a substantially greater number of OTUs and a more even distribution of reads across OTUs within samples. This pattern reflects the broad representation of numerous nematode OTUs with relatively similar read counts, which reduces dominance effects and results in higher calculated evenness values. Effect sizes were large, particularly for richness (Cohen's $d = -5.6$) and Shannon diversity ($d = -4.77$), indicating strong marker-dependent differences in alpha diversity estimates. Overall, the combined patterns of relative number of OTUs and reads (Fig. 2), and alpha diversity metrics (Fig. 3) demonstrate that the choice of genetic marker can substantially influence diversity assessments in meiofauna metabarcoding studies.

Taxonomic composition and diversity contributions differ broadly between gene fragments, potentially reflecting primer selectivity particularly for Nematoda or the influence of the gene divergent degrees on community structure. Compared to COI, V1–V2 provided a more consistent and comprehensive representation of major taxa and avoided some of the common amplification biases and gaps in reference databases associated with COI. Therefore, further comparisons between study sites and between MPAs and adjacent REFs were based on V1–V2 data to ensure robust ecological inference. However, detailed analyses focusing specifically on harpacticoid copepods were performed on both markers.

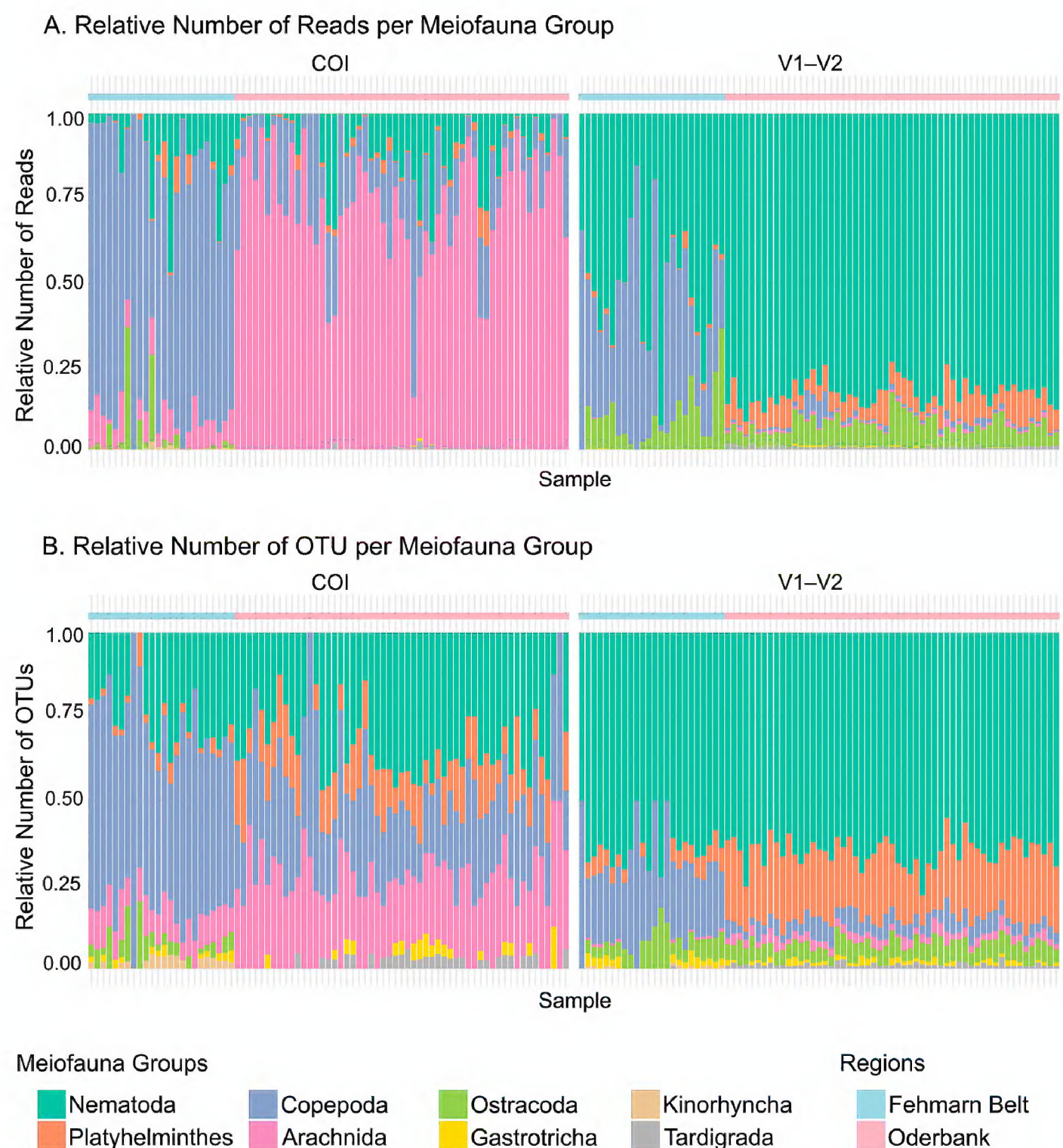


Figure 2. Comparison of the relative number of OTUs and reads per sample across major meiofauna groups based on COI and V1–V2 gene metabarcoding data of the Fehmarn Belt and Oderbank in the Baltic Sea. **A** Relative taxonomic composition (based on the relative number of reads) at the major taxonomic level for each gene fragment. **B** Relative number of OTUs for each meiofauna group and gene fragment. In both panels the left bar plots are reflecting the COI analyses and the right bar plots are referring to the V1–V2 gene fragment. Samples are representing both the Fehmarn Belt and Oderbank, and are ordered by the same treatment structure, allowing for a direct visual comparison of diversity and dominance patterns between the two gene fragments. Color codes are consistent across panels and reflect the meiofaunal taxa and area.

Community patterns across MPAs and REFs

Community composition and diversity patterns varied significantly among regions. Nematoda dominated across all areas, with Copepoda contributing notably in FB REFs, whereas Platyhelminthes were more prevalent in OB (Fig. 4A). OTU richness varied across areas (Fig. 4B), with the MPAs of OB exhibiting the highest median richness, followed by the adjacent REFs of OB, FB, and finally the MPAs of FB. Venn diagrams revealed substantial overlap of OTUs between MPAs and REFs within each region (54.2% shared in FB, 19.0% in OB), but also indicated a notable proportion of unique OTUs associated with either MPAs or REFs particularly in OB (Fig. 4C). These patterns suggest both site-specific and small-scale patchiness of meiofaunal diversity and composition.

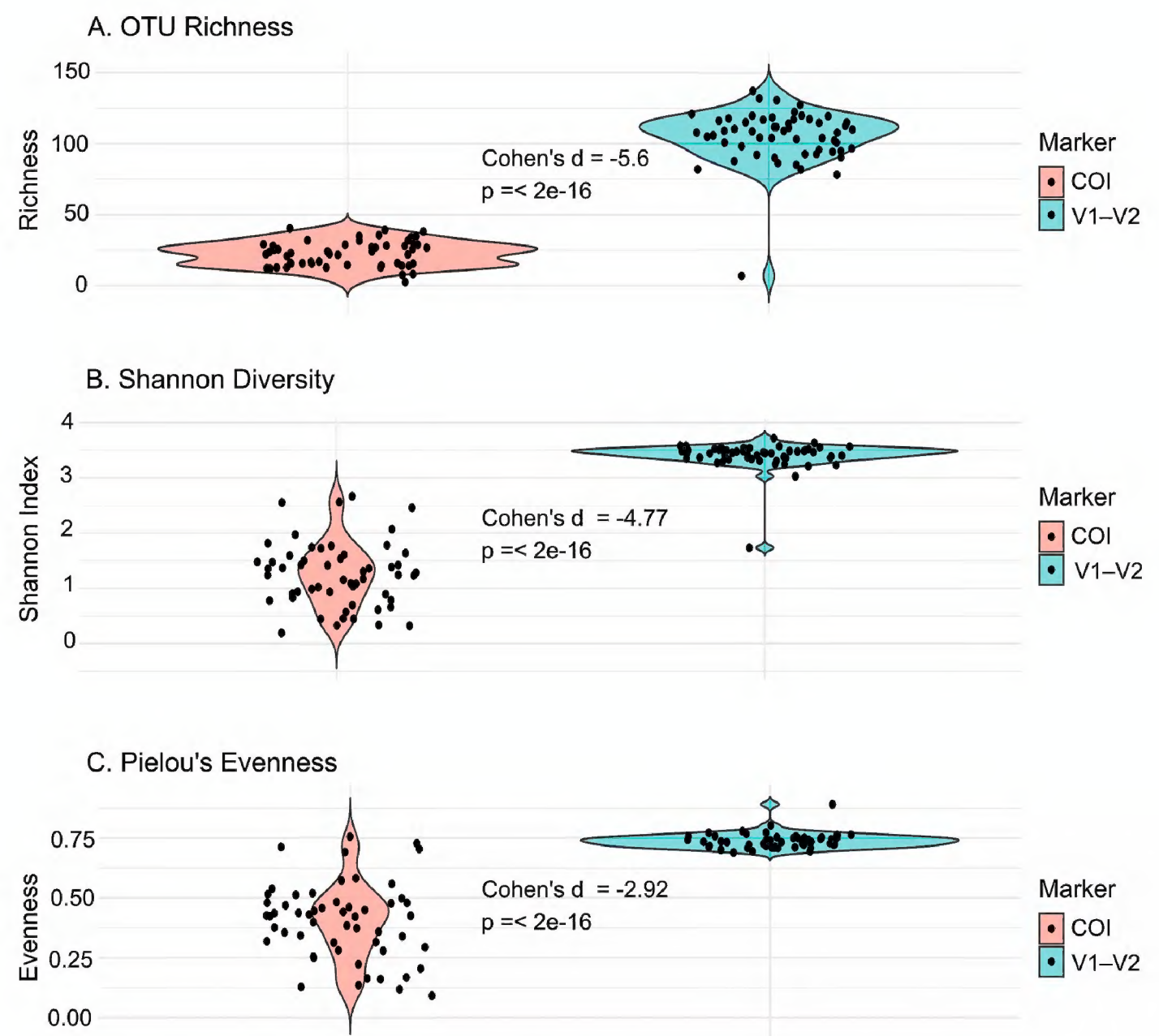


Figure 3. Comparison of alpha diversity metrics between COI and V1–V2 markers across all samples. Violin plots show (A) OTU richness, (B) Shannon diversity, and (C) Pielou's evenness. Black dots represent individual sample values. Statistical significance was assessed using Wilcoxon rank-sum tests; effect sizes are reported as Cohen's d . All three metrics were significantly higher for the V1–V2 marker compared to COI ($p < 2e-16$), with large effect sizes for richness ($d = -5.6$), diversity ($d = -4.77$), and evenness ($d = -2.92$).

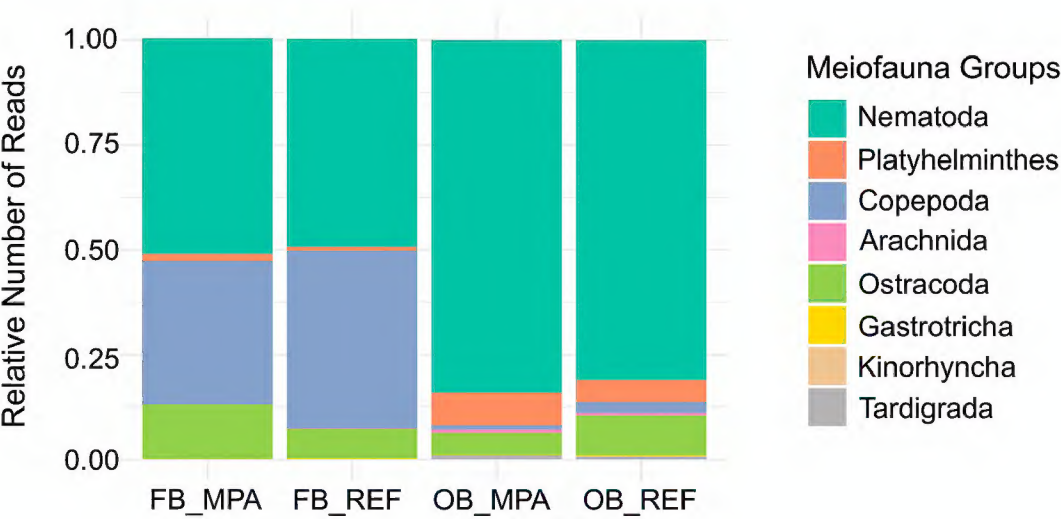
Community composition was compared between the two study sites (PERMANOVA) and between the corresponding MPAs and REFs (pairwise PERMANOVA) using Hellinger-transformed number of reads per OTU with Euclidean distance (Table 1). Community composition differed significantly between FB and OB (PERMANOVA, $p = 0.001$). In the comparison of MPAs and REFs within each site, OB showed significant differences between areas (PERMANOVA, $p = 0.001$), whereas FB did not reveal any significant pattern (PERMANOVA, $p = 0.146$). Across ordination method, non-metric multidimensional scaling (nMDS, based on Hellinger transformed number of reads applying Euclidean distance) showed that samples from FB clustered distinctly from those in OB (Fig. 5A). This separation was especially pronounced along the first nMDS axis, which accounted for the majority of the observed compositional variance between the two sites. Within FB region, samples from MPAs and REFs showed high degree of overlap, while a clear and statistically significant separation was evident in OB (Fig. 5B; Table 1; $p = 0.001$). In FB, PERMANOVA did not detect a statistically significant difference between MPAs and REFs (Fig. 5A; Table 1; $p = 0.146$), which was also apparent from the nMDS ordination.

Overall, these findings indicate that broad geographic differences between FB and OB (likely influenced by factors such as sediment grain size and salinity)

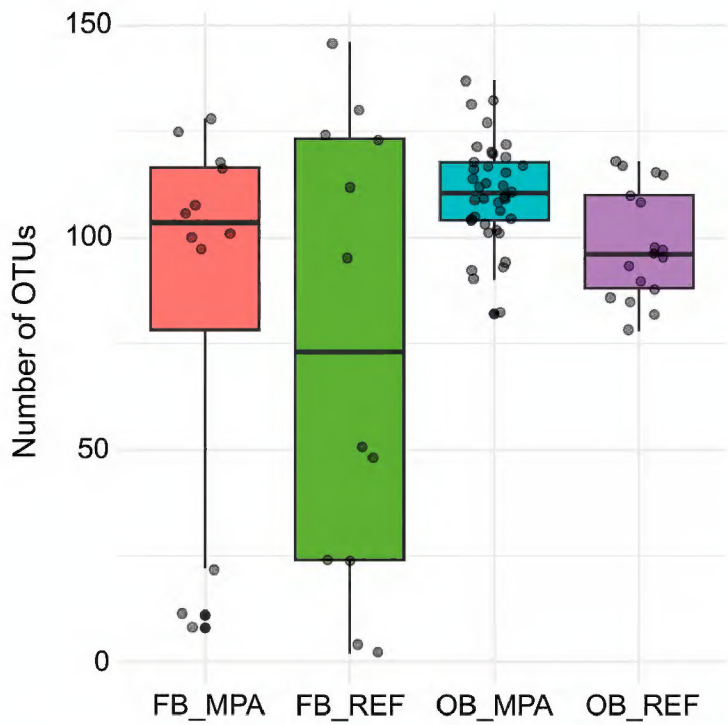
Table 1. PERMANOVA results of meiofaunal community comparisons between regions and areas. The results of PERMANOVA test based on V1–V2 (number of reads per OTU) applying Hellinger transformation and Euclidean similarity index, comparing meiofaunal communities between the two study regions, Fehmarn Belt (FB) and Oderbank (OB), as well as between MPAs and REFs within each region. The table shows degrees of freedom (Df), sums of squares, F. Model, coefficient of determination (R²), p-values, p-values adjusted for multiple comparisons (p.adjusted), and significance codes (Sig). Significant differences are indicated by asterisks: *** p ≤ 0.001 (highly significant); p > 0.1 (not significant).

Pairs	Df	Sums of squares	F.Model	R2	p.value	p.adjusted	Sig
FB vs OB	1	9.0038	67.936	0.46873	0.001		***
FB_MPAs vs FB_REFs	1	0.4302061	1.499804	0.063822	0.146	0.1460	
FB_MPAs vs OB_MPAs	1	5.6277057	57.80773	0.546347	0.001	0.0012	***
FB_MPAs vs OB_REFs	1	4.3504966	32.3307	0.544924	0.001	0.0012	***
FB_REFs vs OB_MPAs	1	4.6713286	39.70179	0.452691	0.001	0.0012	***
FB_REFs vs OB_REFs	1	3.6450763	21.35795	0.441664	0.001	0.0012	***
OB_MPAs vs OB_REFs	1	0.4940963	8.816102	0.142618	0.001	0.0012	***

A. Meiofauna Composition Grouped by Area



B. OTU Richness Grouped by Area



C. Shared and Unique OTUs

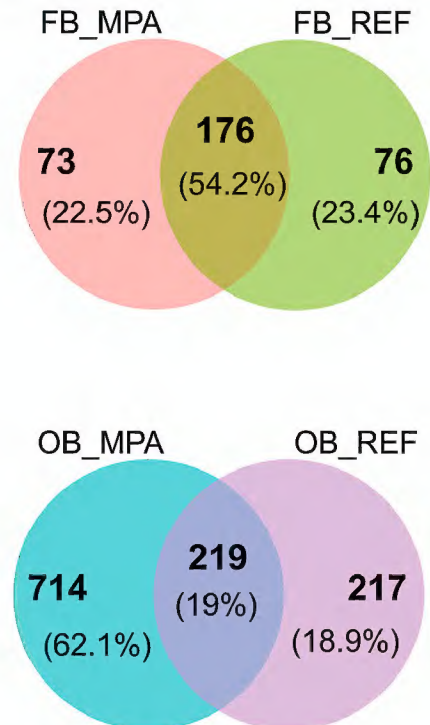


Figure 4. Meiofauna community structure, diversity, and OTU overlap across MPAs and REFs in the Fehmarn Belt (FB) and Oderbank (OB) in the Baltic Sea. **A** Taxonomic composition (relative number of reads) of major meiofaunal groups across sampling sites (FB and OB) and areas MPAs and REFs. **B** OTU richness per sample, grouped by area between the MPAs and REFs. **C.** Venn diagrams showing the number and proportion of shared and unique OTUs between MPA and REF for FB and OB separately.

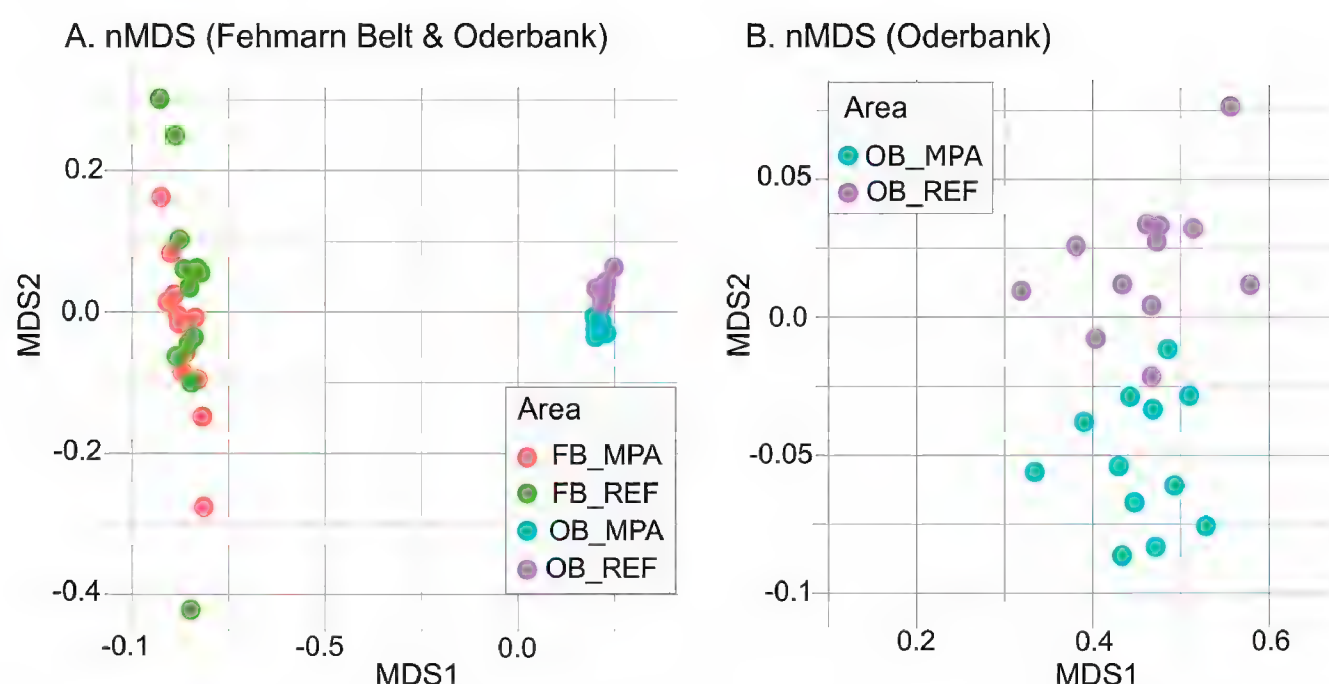


Figure 5. Non-metric multidimensional scaling (nMDS) ordinations of meiofaunal community composition at the OTU level based on V1–V2 metabarcoding data, using Hellinger transformed number of reads and Euclidean distance index. **A** Overall community patterns at both study sites, Fehmarnbelt (FB) and Oderbank (OB), showing the MPAs and REFs within each region. **B** Enlarged view of OB, highlighting the significant differences in community composition between the MPA and REF in this region.

have a strong influence on meiofaunal community structure. Within regions, community composition in the MPAs and REFs of FB did not differ significantly, whereas in OB, the MPAs and REFs showed distinct differences. Considering that trawling had not yet been excluded at the time of sampling, the significant differences observed between MPAs and REFs in OB are likely due to natural spatial patchiness in meiofaunal communities. Since trawling exclusion has now been in place and post-exclusion samples have been collected, both FB and OB provide valuable baseline data for future comparisons aimed at evaluating recolonization and recovery processes following trawling cessation. A list of detected OTUs by each gene marker from all studied stations including taxonomic assignments and related blast values is provided as a Suppl. materials 1, 2.

Method-specific detection patterns and OTU/species-level overlap

Species and OTU richness estimate for harpacticoid copepods varied substantially across methods and regions (Fig. 6A). In FB, morphological analysis yielded the highest median richness per sample, followed by COI and V1–V2 metabarcoding. In contrast, in OB, V1–V2 and COI revealed similar OTU richness, both slightly higher than morphology. Despite these differences, all three methods consistently detected higher harpacticoid diversity in FB.

Species/OTU accumulation curves reflected these patterns (Fig. 6B), with richness in FB approaching an asymptote, particularly for COI and morphology. In both areas, however, accumulation curves for V1–V2 continued to rise steeply, suggesting incomplete sampling saturation, whereas COI and morphology reached lower plateaus, especially in OB. Individual samples occasionally showed discrepancies, with either morphological richness exceeding molecular estimates or vice versa, highlighting the different sensitivities and detection biases of each method. At OB, morphology detected the fewest harpacticoid species (Ostmann unpubl. data1), likely due to a higher occurrence of unidentifiable juvenile stages and the effects of elevated intraspecific variability.

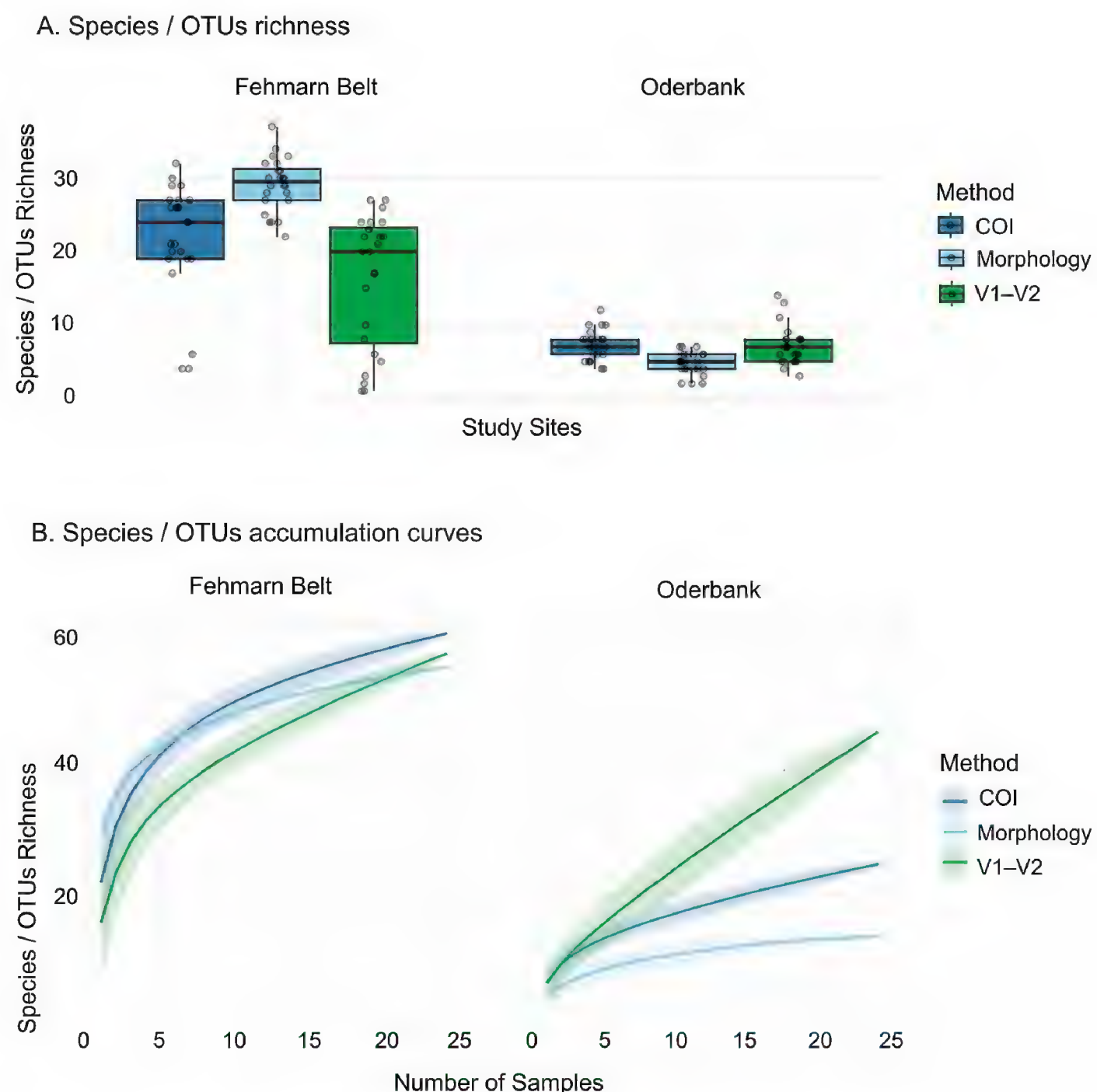
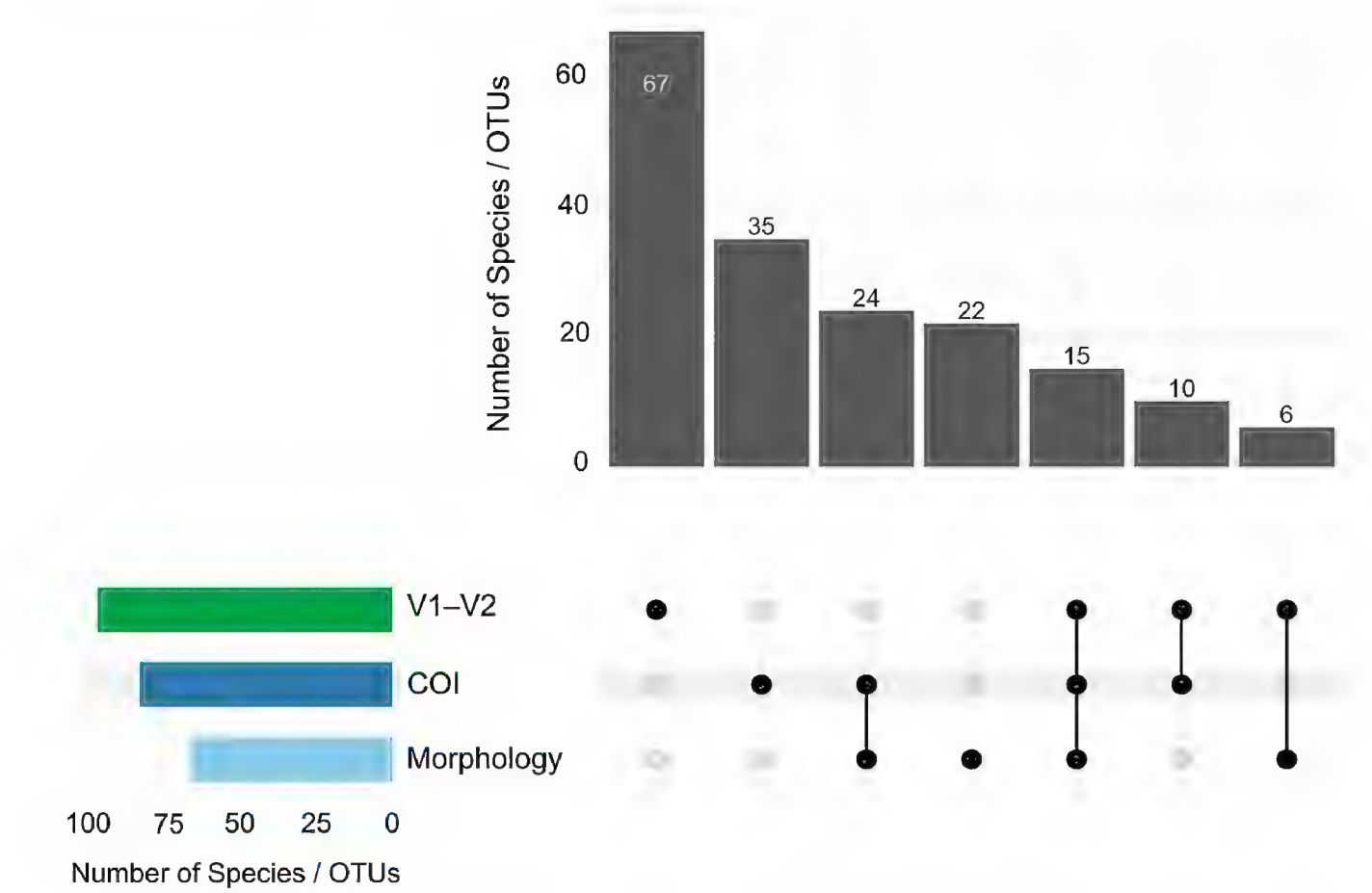


Figure 6. Species/OTU richness patterns for harpacticoid copepods by detection method and study site. **A** Boxplots showing species/OTU richness per sample in Fehmarnbelt (FB) and Oderbank (OB) for morphology, COI, and V1–V2 metabarcoding. **B** Species/OTU accumulation curves for each method within FB and OB, with shaded areas indicating 95% confidence intervals.

Both COI and V1–V2 recovered distinct OTUs, but COI showed greater overlap with morphology among the most frequently detected taxa. The UpSet plot (Fig. 7A) illustrates these relationships across all detected harpacticoid members (OTUs with ambiguous assignments such as “Harpacticoida-environmental-DNA” were excluded from this analyses). COI and morphology shared 24 OTU/species, whereas V1–V2 and morphology shared only 6. Each method also detected unique taxa: V1–V2 yielded 67 exclusive taxa, COI identified 35, and morphology detected 22. Among the top 20 most frequently detected harpacticoid taxa per method, 13 were consistently observed across all approaches (Fig. 7B), such as *Laophonte longicaudata reducta* Lang, 1936, *Halectinosoma curticorne* (Boeck, 1873), *Danielssenia typica* Boeck, 1873, *D. quadriseta* Gee, 1988, *Proameira* sp. Lang, 1944, *Tachidiella minuta*, *Cletodes tenuipes* Scott T., 1897, *Amphiascoides dispar* (Scott T. & Scott A., 1894), and *Tachidius (Tachidius) discipes* Giesbrecht, 1881 (species shared across methods are indicated by black outlines in Fig. 7B). Although COI- and V1–V2-based taxonomic assignments were validated against a curated reference library of identified harpacticoid specimens, some morphologically observed species may not have been represented in the barcode

A. Shared and Unique Species / OTUs between Methods



B. Top 20 Most Frequently Detected Species / OTUs by Methods

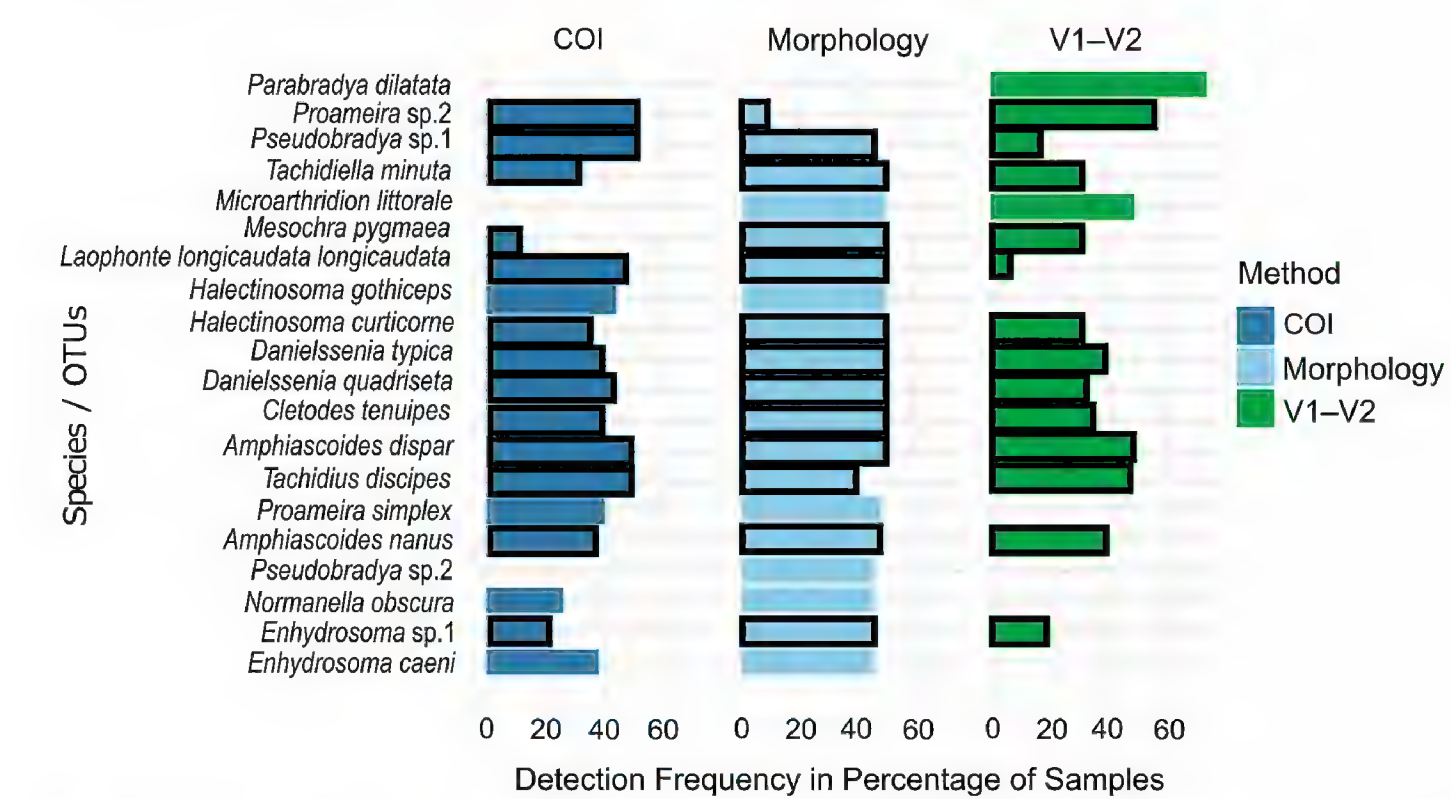


Figure 7. Shared and unique harpacticoid species/OTUs detected by morphology, COI and V1–V2 metabarcoding. **A** UpSet plot showing the number of unique and shared harpacticoid taxa among methods, with the bar chart at the top indicating counts for each combination. Linked dots under the bar chart show which methods are compared in the bars above. Coloured bars on the left show total numbers of species/OTUs. **B** Top 20 most frequently detected harpacticoid species/OTUs per method, with black outlines indicating species detected by all three methods.

database, especially those encountered only once during morphological analyses. Additionally, not all identified species yielded high-quality barcode sequences suitable for inclusion in the reference dataset. As a result, certain taxa may have gone undetected in the molecular datasets or may have been assigned to closely related species already present in the database or NCBI. Several species, such as *Parabradia dilatata* (Sars, 1904), *Pseudobradia* sp.,

Cletodes tenuipes, and *Nannopus palustris* Brady, 1880, were associated with multiple OTUs by both markers, especially in the V1–V2 dataset. This may be due to the presence of non-adult stages (e.g., nauplii, copepodids), which are challenging to identify morphologically and often absent from reference barcode libraries. Consequently, they are underrepresented in morphological datasets but still detected by metabarcoding. Without exact reference matches, these sequences are assigned to the closest related species in the database, potentially producing multiple OTUs with the same species name.

Similarity analyses further showed that COI and morphology had the highest overlap in species detection (Sørensen = 0.517; Jaccard = 0.348), whereas V1–V2 exhibited lower similarity with both COI (Sørensen = 0.275; Jaccard = 0.159) and morphology (Sørensen = 0.255; Jaccard = 0.146), indicating limited taxonomic overlap. Overall, COI provided greater OTU-level resolution for harpacticoid copepods, making it particularly useful for targeted taxonomic assessments. These findings highlight the complementary nature of molecular and morphological approaches, with each contributing unique as well as overlapping insights into harpacticoid diversity. A complete list of harpacticoid species and OTUs (including number of individuals and sequencing reads) detected by each method across both regions is provided in Suppl. material 3: Harpacticoida species/OTU table, with OTUs assigned to the same species distinguished by numerical suffixes.

Discussion

This study provides one of the first integrated assessments of meiofauna communities across marine protected areas (MPAs) and adjacent reference areas (REFs) in the Baltic Sea using a multi-marker metabarcoding approach alongside morphological identification of harpacticoid copepods. By applying both mitochondrial COI and ribosomal 18S (V1–V2) markers, we were able to capture complementary signals of meiofaunal diversity and evaluate spatial community dynamics in designated MPAs/REFs and broader regional differences within the two study regions Fehmarn Belt and Oderbank. Across both marker datasets, more than 1,700 meiofauna OTUs were detected, spanning key meiofaunal phyla such as Nematoda, Copepoda, Arachnida (only Acari), Platyhelminthes, Gastrotricha, Kinorhyncha and Tardigrada. COI data revealed a pronounced dominance of Arthropoda, particularly copepods, while the 18S marker recovered a more balanced representation of meiofauna phyla, including higher proportions of Nematoda and various less-abundant groups.

Species level analyses of harpacticoid copepods revealed highest congruence between COI metabarcoding and morphology. Both methods shared a core group of frequently occurring species known as abundant harpacticoid taxa in the studied areas (also recorded as the most abundant taxa by Packmor et al. (2025) in Fehmarn Belt), including *Danielssenia typica*, *Microarthridion littorale*, *Cletodes tenuipes*, *Laophonte longicaudata minuta*, and *Amphiascoides dispar* (Scott T. & Scott A., 1894). However, both methods also captured unique taxa; morphology revealed additional rare or undescribed copepods, while metabarcoding detected OTUs potentially representing cryptic or juvenile forms, often overlooked microscopically. This demonstrates how the combination of methods enables a more comprehensive view of biodiversity.

Marker-specific insights into meiofaunal diversity

Our results clearly demonstrate that marker choice substantially affects the perception of community structure and diversity. The V1–V2 fragment consistently revealed higher OTU richness, Shannon diversity, and Pielou's evenness compared to COI across nearly all samples. It also provided broader taxonomic coverage, recovering more taxa from certain meiofaunal groups such as Nematoda, Platyhelminthes and Ostracoda. Only mites had a higher number of taxa detected by the COI marker. This aligns with previous findings (e.g. Vanhove et al. 2013; Macheriotou et al. 2019; Ficetola et al. 2024), which reported high amplification success and broad eukaryotic coverage across most 18S primer sets (including what has been used in our study), with limited specificity toward nematodes. Our detection of nematode diversity from the 18S dataset also mirrors results from Wang et al. (2023), who observed that the 18S marker efficiently recovered nematodes, cercozoans, and other protists from intertidal sediments, but that resolution at the species level was often lacking.

In contrast, COI detected fewer overall OTUs, but offered superior resolution within certain taxa most notably Harpacticoida. This specificity proved especially valuable for species-level comparisons between MPAs and REFs. Our results confirm the better species delimitation ability of COI reported by Tang et al. (2012), who found that COI estimated over seven times more putative species than 18S and aligned better with morphospecies boundaries. Similarly, Derycke et al. (2010) demonstrated that the I3-M11 COI region successfully differentiated closely related marine nematode species, with higher amplification success than the Folmer region (Folmer et al. 1994) which was targeted in our study. Despite these benefits, the COI data offered a narrower taxonomic scope, enhancing detection of copepods but overlooking many other meiofauna groups possibly due to primer bias or gaps in reference sequences. Primer-related biases were evident when comparing results across taxa: while COI detected high diversity among copepods, groups such as Nematoda and Platyhelminthes were poorly represented. This trend was also noted by Atherton and Jondelius (2020), who found that COI underestimated platyhelminth diversity compared to 18S and that many flatworm OTUs remained unassigned due to incomplete barcode libraries. These findings emphasize the limitations of COI when applied without a curated reference database, especially for taxa with high intraspecific variability or few publicly available sequences. Our use of both mitochondrial and nuclear markers provided critical complementarity. Giebner et al. (2020) also recommended a dual-marker approach after comparing a DNA sequence-capture method for COI and 18S to conventional metabarcoding of those same fragments. They found that sequence capture recovered substantially more taxa (especially rare or cryptic species) than metabarcoding alone, and that using two markers in parallel for metabarcoding further increased the likelihood of detecting true diversity. Together, these studies support our approach, highlighting the value of using multiple markers to mitigate individual limitations and achieve a more holistic view of meiofaunal diversity. Similar conclusions were drawn by Pawlowski et al. (2018), who have consistently emphasized the importance of integrating multiple markers in eDNA metabarcoding to improve biodiversity assessments in marine environments. Their work has demonstrated that combining COI and 18S rDNA not only enhances taxonomic coverage specifically reported for protists

(Pawlowski et al. 2016) but also supports the development of DNA-based biotic indices for ecological monitoring (Pawlowski et al. 2018).

Although in our study the read numbers were used as a proxy for relative abundances when calculating alpha diversity metrics, we acknowledge that sequencing reads do not necessarily reflect true organismal abundances. Variations in body size, gene copy number, primer affinity, and amplification efficiency can bias the number of reads per taxon. In this study, however, only bona fide meiofaunal taxa with broadly comparable body sizes were considered, which minimizes extreme differences in template DNA quantity across taxa driven by body mass. Therefore, while read numbers cannot be equated directly with absolute abundances, they are considered a reasonable proxy for the relative abundances of taxa within samples in this dataset. This interpretation is further supported by empirical evidence from Rossel et al. (2019), who demonstrated that, when using a complete reference library and applying appropriate data transformations, read numbers per OTU reliably reflect relative species abundances in metabarcoding analyses.

In addition, our data extend previous observations to the context of Baltic Sea meiofauna—an environmentally variable and still understudied region, demonstrate that metabarcoding represents a robust alternative to time-intensive traditional analyses for ecological monitoring and emphasize the importance of selecting genetic markers according to specific study objectives—whether focused on community-wide surveys, taxon-specific assessments, or functional monitoring.

Spatial structuring of meiofauna at the MPAs and REFs

Our comparative analysis between FB and OB revealed a clear spatial structuring of meiofaunal communities. This was consistently supported by PERMANOVA results and ordination plots—particularly for the 18S dataset and morphological data. The regional signal was strong, with distinct clusters forming between FB and OB across all taxonomic levels. These differences in meiofauna community are likely driven by environmental gradients such as sediment grain size, organic content, and salinity, which vary substantially between the two regions, as documented in the MGF-Ostsee project reports (Gogina and Schönke 2020; Feldens et al. 2021). Similar patterns have been observed elsewhere: Wang et al. (2023) showed that salinity and sediment composition were key predictors of intertidal meiofaunal community shifts in the Yellow Sea. In our study, the contrasting diversity and assemblage patterns between FB and OB may reflect the environmental differences between the two regions. FB sediments contain a much higher proportion of fine particles ($<62.5\ \mu\text{m}$; $\sim 50\%$ in FB compared to $\sim 0.5\%$ in OB), substantially higher organic matter content ($\sim 6\%$ in FB vs. $\sim 0.4\%$ in OB), and higher salinity (Gogina and Schönke 2020; Feldens et al. 2021). These differing conditions might contribute to the distinct meiofaunal assemblages observed in the two areas. Comparable environmentally driven patterns have been reported for sublittoral habitats in the southern North Sea and Baidaratskaya Bay of the Kara Sea, where depth and sediment type strongly influenced meiofaunal composition (Udalov et al. 2017; Schratzberger et al. 2000). Further support for the role of sediment characteristics comes from recent assessments of sediment-disturbed environments. Kapshyna et al. (2024) suggested that meiofaunal community differences can arise from sediment mismatches caused by grain-size variation following nourishment events. They noted that increases in the quantity

and heterogeneity of coarser sediments can positively affect post-impact meiofaunal abundances and richness (see also Glueck 2023; Fegley et al. 2020). This aligns well with our findings, underscoring that even moderate shifts in sediment texture can substantially influence meiofaunal community structure.

In addition, we observed statistically significant differences (PERMANOVA test) between MPAs and REFs at OB. Given that fisheries exclusion had not yet been implemented at the time of sampling, these differences are likely attributable to the naturally patchy distribution of meiofaunal communities. This interpretation is consistent with the observations of Folkers and George (2011), who documented habitat partitioning among harpacticoid species in the western Baltic sublittoral, suggesting that substantial species turnover can occur over relatively short spatial scales. In contrast, we detected no significant differences in the meiofauna community between areas within the Fehmarn Belt, in line with the findings of Packmor et al. (2025), who also reported no significant differences between MPAs and REFs when comparing meiofauna communities at major taxonomic levels. Our study was conducted in proposed MPAs and REFs to evaluate their suitability for future protection measures and the contrasting results between FB and OB underscore the importance of spatially explicit, context-aware assessments when evaluating MPAs effectiveness after exclusion of fishery. As fisheries exclusion had been implemented neither in FB nor in OB at the time of sampling, our study represents the 'Before' phase of a BACI-style (Before-After-Control-Impact) framework. By incorporating proposed MPAs and adjacent REFs, our design establishes a critical ecological baseline to assess future impacts of trawling exclusion. As Seger et al. (2021) emphasize, BACI designs are essential for disentangling natural variability from human-induced effects. Our data serve as a foundational reference point for upcoming 'After' assessments, enabling robust evaluations of fauna turnover and potential recovery. In this way, our study complements similar BACI-based initiatives (Gogina and Schönke 2020; Feldens et al. 2021) that aim to assess the ecological effectiveness of trawling bans and broader conservation interventions in Baltic MPAs.

Congruence and complementarity of morphology and metabarcoding

Our detailed comparison of morphological and molecular data for harpacticoid copepods revealed both complementary strengths and notable discrepancies. In FB, morphological analysis recovered a higher number of species per sample, particularly less abundant taxa such as *Normanella obscura* Lee W. & Huys, 1999, *Stylicletodes longicaudatus* (Brady & Robertson, 1876), *Haloschizopera pygmaea* (Norman & Scott T., 1905), and *Monopenicillus anke* George, Zey & Packmor, 2023. These species were absent from one or both metabarcoding datasets, likely due to PCR bias, inefficient DNA extraction, or the absence of reference barcodes. Conversely, both metabarcoding methods detected several potential cryptic species-level OTUs, for example, within *Cletodes tenuipes*, *Enhydrosoma curticauda*, *Tachidius discipes* Giesbrecht, 1881, *Nannopus palustris*, *Pseudobradya* sp. and *Parabradya dilatata*. Notably, the last taxa were detected only by the V1–V2 marker and were absent from the morphological and COI dataset, possibly because the V1–V2 region is relatively conserved, limiting its ability to discriminate among closely related species. These findings align with those of Rossel and Martínez Arbizu (2019), where morphological and MALDI-TOF mass spectra data revealed several distinct lineages within the harpacticoid community of the North Sea, the specimens of *N.*

palustris from different seas (Garlitska et al. 2012) and several other harpacticoid species (e.g., Rocha-Olivares et al. 2001; Vakati et al. 2019). In our study, while the overlap between methods was strong, it remained incomplete. Several dominant taxa—including *Danielssenia typica*, *Halectinosoma gothiceps*, and *Cletodes tenuipes*—were consistently detected by both approaches, underscoring their ecological relevance and confirming the robustness of both methods while method-specific detections also revealed technical limitations: morphology may overlook small, fragile, or early-stage individuals, whereas molecular methods may miss taxa due to primer binding biases or gaps in reference databases, as also noted by Zeppilli et al. (2015). When comparing individual gene fragments to morphology, the V1–V2 marker failed to detect certain taxa—such as *Proameira simplex* (Norman & Scott T., 1905) and *Echinolaophonte horrida* (Norman, 1876)—that were abundantly recovered through morphology and COI. This might highlight the limited resolution of the V1–V2 fragment for species-level discrimination. Similar method-specific differences were documented in different multi-gene studies e.g., Bucklin et al. (2016), Cahill et al. (2018) and Gielings et al. (2021), where both approaches captured broad-scale community patterns but varied in taxonomic depth and precision. Many studies such as Aylagas et al. (2014), Bucklin et al. (2021) and Gielings et al. (2021) further emphasized the value of integrating morphological expertise with molecular tools to achieve accurate and reproducible biodiversity assessments.

Implications for monitoring and conservation

This study reinforces the value of meiofauna as indicators for ecological monitoring in marine systems. Our observation of region-specific OTUs, significant community differences between sites, and sensitivity of certain copepod taxa to environmental conditions point to the ecological signal contained within these small-bodied yet functionally important organisms, aligning with other related studies (Bik et al. 2012; Fonseca et al. 2017). As Zeppilli et al. (2015) argue, meiofauna possess several ideal traits for biomonitoring, including ubiquity, short generation times, and diverse functional roles. From a methodological standpoint, our findings reiterate the importance of accurate reference databases and tailored marker selection. The limitations encountered with COI—particularly for underrepresented taxa like nematodes and platyhelminths—highlight the need for using broader gene fragments and ongoing reference library development for different taxon groups (also indicated by Sinniger et al. 2016; Gielings et al. 2021; Ficetola et al. 2024). In the Baltic Sea, where novel or cryptic species are frequently encountered (Packmor et al. 2025), such efforts are particularly urgent. The integration of molecular tools into routine ecological monitoring has been recommended by other studies, emphasizing the scalability of metabarcoding and the potential of molecular approaches to detect ecosystem change across diverse spatial and temporal scales (e.g. Pawlowski et al. 2016; 2018). Incorporating such frameworks could significantly enhance meiofaunal monitoring programs in the Baltic and other dynamic marine systems.

Our data demonstrate that MPAs can serve as valuable biodiversity reservoirs, even for organisms that are rarely considered in conservation assessments. As marine protection strategies evolve, integrating meiofaunal data into long-term monitoring programs—particularly using metabarcoding—can enhance detection of ecosystem change and improve management outcomes.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

Sampling and field studies: All necessary permits for sampling and observational field studies have been obtained by the cruise leader of EMB238 and 267 from the competent authority (Bundesamt für Seeschifffahrt und Hydrographie (BSH)).

Use of AI

English wording was polished using ChatGPT (OpenAI), when needed.

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Data availability

The metabarcoding raw sequence data are publicly available in the NCBI Sequence Read Archive (SRA) under BioProject ID PRJNA1309109, with SRA accession numbers SRR35078194–SRR35078336. The OTU tables generated for each genetic fragment are provided as Suppl. materials 1, 2, where the first 21 columns include detailed taxonomic

information for each OTU, including NCBI accession numbers (“accn”), BLASTn percentage identity (“pident”), query coverage (“qcov”), and E-value (“eval”). A list of harpacticoid species and OTUs detected by each method (Morphology, COI, and V1–V2) is available in Suppl. material 3. In this table, columns correspond to species/OTU names (“Species”), morphologically detected species in Fehmarn Belt and Oderbank (“Morphology_FB” and “Morphology_OB”), and OTUs detected by each fragment (COI and V1–V2) in each study area (“COI_FB”, “COI_OB”, “V1–V2_FB”, and “V1–V2_OB”). The study is compliant with CBD and Nagoya protocols.

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Supplementary material 1

V1–V2 OTU table

Authors: Sahar Khodami, Alexandra Ostmann, Jana Packmor, Kai Horst George, Pedro Martínez Arbizu

Data type: csv

Explanation note: A list of detected OTUs by V1–V2 gene marker from all studied stations including taxonomic assignments and related blast values. The first 21 columns include detailed taxonomic information for each OTU, including NCBI accession numbers (“accn”), BLASTn percentage identity (“pident”), query coverage (“qcov”), and E-value (“eval”).

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Link: <https://doi.org/10.3897/mbmg.9.169630.suppl1>

Supplementary material 2

COI OTU table

Authors: Sahar Khodami, Alexandra Ostmann, Jana Packmor, Kai Horst George, Pedro Martínez Arbizu

Data type: csv

Explanation note: A list of detected OTUs by COI gene marker from all studied stations including taxonomic assignments and related blast values. The first 21 columns include detailed taxonomic information for each OTU, including NCBI accession numbers (“accn”), BLASTn percentage identity (“pident”), query coverage (“qcov”), and E-value (“eval”).

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Link: <https://doi.org/10.3897/mbmg.9.169630.suppl2>

Supplementary material 3

Harpacticoida species/OTU table

Authors: Sahar Khodami, Alexandra Ostmann, Jana Packmor, Kai Horst George, Pedro Martínez Arbizu

Data type: csv

Explanation note: A complete list of harpacticoid species and OTUs detected by each method (Morphology, COI and V1–V2) across both regions is provided here. OTUs assigned to the same species names are distinguished by numerical suffixes.

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